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Linking individual behaviour and migration success in *Salmo salar* smolts approaching a water withdrawal site: implications for management

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Abstract – Seaward migration of immature salmonids (smolts) may be associated with severe mortality in anthropogenically altered channels. Few studies however, have identified distinct behaviours that lead to exposure to adverse habitats or even unsuccessful migration. This study used high resolution telemetry to map migration routes of Atlantic salmon (*Salmo salar*) smolts approaching a water withdrawal zone associated with an aquaculture facility in a lowland river. Individual smolts were tagged with an acoustic transmitter and released upstream of the water withdrawal zone. A trap was installed downstream of the water withdrawal zone. The trap captured all smolts that passed the water withdrawal zone. The tracking results confirmed previous studies on Pacific salmon showing that Atlantic salmon smolts may perform milling behaviours (i.e. upstream excursions and circular swimming behaviour) in anthropogenically altered channels. Non-milling and milling smolts were compared. Smolts performing milling behaviours covered a larger area (m²) and experienced an increased probability of entering the water withdrawal zone, considered an adverse habitat. Finally, smolts were identified as either passing (67%) or non-passing (33%) the water withdrawal zone based on the recapture data from the trap. In total, 20% of the non-passing smolts entered the aquaculture facility. Several behavioural traits differed between the remaining (80%) non-passing smolts and the passing smolts. In particular, time spent near the water withdrawal zone correlated negatively with the probability of passage. These links between individual behaviours and exposure to adverse habitats and passage probability may be applied to improve management of salmonid populations.

Key words: Anadromous fish / Fish farm / Fish passage / Fisheries / HTI / Migratory delay / Salmonidae / Telemetry

1 Introduction

Dam building in rivers and streams has occurred globally for decades (Roscoe and Hinch 2010; Johnsen et al. 2011). In potamodromous and diadromous fishes, dams and weirs often delay or inhibit access to spawning (Gehrke et al. 2002; Gosset et al. 2006), nursery (Saunders 1960; Arnekleiv and Rønning 2004) and foraging (Agostinho et al. 2002; Aarestrup and Koed 2003) areas. Impeded migration may lead to fragmentation effects on the genetic structure (Meldgaard et al. 2003; Heggenes and Røed 2006) and even genetically depauperate fish populations (Hansen and Jensen 2005). Blocked

migration may result in extirpation of the most vulnerable populations (Aarestrup and Jepsen 1998; Gehrke et al. 2002).

Water withdrawal represents one of the most severe anthropogenic alterations of fish habitats (Parrish et al. 1998) and may result in a substantial percentage of juvenile migrants being lost from rivers (Aarestrup and Koed 2003; Unwin et al. 2005). The loss may be up to 70% when migrants are passing water withdrawal zones in lowland rivers (Aarestrup and Koed 2003). The mechanisms underlying the severe losses of fishes migrating through anthropogenically altered channels are not fully understood (Olsson et al. 2001; Aarestrup and Koed 2003). While several studies have documented migratory delays and cessation of migration (Olsson et al. 2001; Aarestrup and Koed 2003), few studies have examined how

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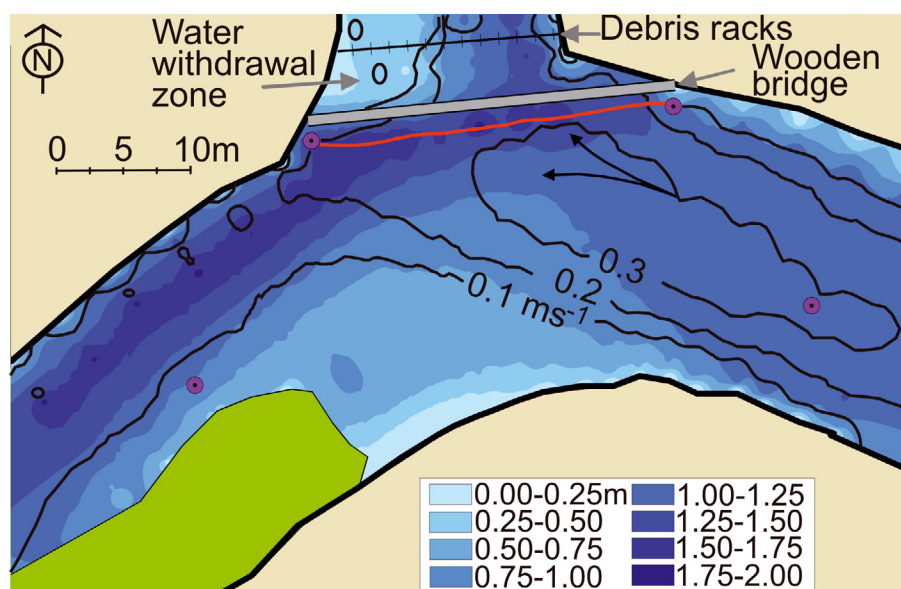


Fig. 1. Schematic map showing the hydrophone array and water withdrawal zone. Hydrophones are indicated by purple symbols. Black arrows show the flow direction and the diversion of water to the fish farm. Water diverted to the fish farm drained under the wooden bridge and through the debris racks. The area between the wooden bridge and debris racks was termed the water withdrawal zone. The colour bars indicate the water depths (m). Current velocities (m s^{-1}) are indicated by the contour lines. The shore line is illustrated using a thick black line, while the green area in the lower left corner indicates emergent vegetation. Acoustic transmitters were towed between hydrophones to verify system precision and accuracy. A tow track between the two northernmost hydrophones is illustrated using a red line. Tagged smolts were released 200 m. upstream of the water withdrawal zone (not shown). A Wolf trap was installed at a weir 90 m downstream of the water withdrawal zone (not shown).

individual behaviours translate into exposure to adverse habitats or even unsuccessful migration. Knowledge in this field is crucial to improve the passage probability of fishes migrating in anthropogenically altered channels (Schilt 2007; Zabel et al. 2008; Brown et al. 2009).

Downstream migrating immature salmonids (smolts) may perform milling behaviours (i.e. upstream excursions and circular swimming behaviour) in anthropogenically altered channels (Venditti et al. 2000; Plumb et al. 2006; Nestler et al. 2008), however few studies have examined the consequences of these behaviours. The present study had two purposes. First, non-milling and milling smolts were compared to test the hypothesis that milling Atlantic salmon (*Salmo salar*) smolts would cover a larger area (m^2) and experience an increased probability of entering adverse habitats. Second, this study quantified the behavioural underpinnings of successful and unsuccessful passage of a water withdrawal site. By examining these relationships, the present study aimed at improving management of salmonid populations migrating through anthropogenically altered channels.

2 Materials and methods

2.1 Field site

The Konge River drains into the Wadden Sea in western Denmark. It is 70 km long and has an average slope of 0.5‰. The mean annual discharge is approximately $7 \text{ m}^3 \text{ s}^{-1}$ at the outlet. The river is predominantly 8–15 m wide and 0.5–1.4 m

deep. The Konge River supports a population of anadromous Atlantic salmon recovering from previous habitat degradation and pollution. The Jedsted Mill Fish Farm (55° 23' N; 8° 43' E) is situated 7 km upstream of the Wadden Sea. The present study was carried out upstream of a standard sharp-crested weir (Haro et al. 1998) associated with the fish farm. Water for the fish farm is diverted from the river 90 m upstream of the weir, drains under a wooden bridge and through debris racks (Fig. 1). The zone between the wooden bridge and the debris racks was termed the water withdrawal zone (Fig. 1). Ponds with mature rainbow trout (*Oncorhynchus mykiss*) are found on the downstream side of the debris racks. Additional study site details have been published previously (Svendsen et al. 2010).

Employing a backpack GPS (Model TSC 1; Trimble, Damon, USA) and a portable anemometer (Model C2; OTT; Kempton; Germany), bathymetry and velocity maps were constructed (Fig. 1). Data were collected using methods reported previously (Olsson et al. 2001; Kanno and Voroun 2010).

A Wolf trap (Wolf 1951) (apertures 8 mm, inclination 1:10; Jonsson and Jonsson 2002) was installed at the weir, downstream of the water withdrawal zone (Fig. 1). The trap captured all downstream migrating Atlantic salmon $\geq 10 \text{ cm}$ (Jonsson et al. 1998; Svendsen et al. 2010). The trap was emptied at least daily until the end of the smolt migration period.

2.2 Tracking equipment

Atlantic salmon smolts were tracked 2-dimensionally (i.e. x , y coordinates) using an array of four hydrophones

(Hydroacoustic Technology Inc., Seattle, USA) positioned near the water withdrawal zone (Fig. 1). The hydrophones were connected to an acoustic receiver (Model 291) (Ehrenberg and Steig 2002, 2003) and placed in a square-like configuration (Fig. 1). Acoustic signals were marked manually and developed using the software MarkTags version 3.00 beta c and AcousticTag version 3.10. Data acquisition employed temperature-corrected sound speeds (to nearest 0.01 °C). To verify system performance, acoustic transmitters (Model 795E; mass: 1.6 g; length: 20 mm; diameter: 6.5 mm; 307 kHz; output power level: 155 dB re 1 μ Pa @ 1 m; transmission frequency: 0.51–0.44 Hz; expected operation period \geq 11 days) were towed between fixed hydrophones. The tests indicated that transmitters were positioned with an accuracy and precision < 1 m within the hydrophone array (Fig. 1). These observations are in agreement with previous studies (Semmens 2008; Brown et al. 2009). The hydroacoustic equipment was capable of tracking several transmitters (≥ 15) inside the hydrophone array simultaneously. The hydrophone array was in operation until the end of the smolt migration period.

2.3 Tagging and release

During the spring, indigenous Atlantic salmon smolts from the trap were anaesthetised and tagged with an acoustic transmitter (Model 795E) surgically implanted into the body cavity. Similar to past studies (Johnson et al. 2010), no fish smaller than 17 cm were equipped with a transmitter to keep the ratio transmitter mass: smolt mass low. All fish selected for tagging came from the trap and were considered actively migrating smolts based on morphological characteristics. Silvery appearance, enlarged eyes and length-weight relationship were used as indicators of smoltification (Hoar 1988). There was no evidence of fish approaching a desmoltification stage. Anaesthesia and surgery procedures followed the same protocol as previous studies (Thorstad et al. 2004; Finstad et al. 2005). During anaesthesia, the total length and mass of each fish were measured (to nearest 1 mm and 0.1 g, respectively). After operative recovery, fish were released 200 m upstream of the hydrophone array following Svendsen et al. (2010). Smolts are typically nocturnal migrants (Olsen et al. 2004; Svendsen et al. 2007). Therefore, to reduce the risk of post release predation and facilitate nocturnal migration, fish were released in darkness (i.e. ≥ 2 h after sunset). Fish were released in groups of 4–15 individuals. A total of 79 smolts was captured, tagged and released over a period of 18 days (April 27–May 14).

The released smolts were presumably offspring (age $\geq 2+$) of wild Atlantic salmon spawning in the Konge River. The possibility remains however that the smolts originated from stocking of juvenile fish (age 1+; total length: 8 cm (range 6–12.5 cm). Stocking in the river is based on F1 Atlantic salmon that are indigenous to the area (i.e. supportive breeding).

2.4 Data acquisition

Atlantic salmon 2D coordinates were analysed using a script written in Mathematica version 4.0.2.0 for Windows

(Wolfram Research, Champaign, USA). To ensure high accuracy and precision of the coordinates used for the analyses, the script only considered data from the zone delimited longitudinally by the hydrophones positioned furthest upstream and downstream (Fig. 1). The following refers to this limited area as the hydrophone array. Using individual fish within the hydrophone array, the script determined the duration, the distance migrated and the mean travel speed. The mean travel speed was calculated as the total distance migrated divided by the duration. The measurements were not corrected for current velocity. In addition, the number of visits to the hydrophone array was determined. Finally, using a line running along the wooden bridge, the script determined if fish entered the water withdrawal zone (Fig. 1).

There is a negative correlation between the distance from the hydrophone array and the probability of a 2D coordinate (Ehrenberg and Steig 2002, 2003). Hence, the likelihood of a ping from a tagged fish situated outside of the hydrophone array resulting in a 2D coordinate is reduced. This means that fish may occasionally leave the hydrophone array without generating a 2D coordinate outside of the array. To determine the number of visits individual fish performed to the hydrophone array, it was crucial to know when a fish was outside of the hydrophone array. Similar to Brown et al. (2009), preliminary data indicated that a tagged fish was situated outside of the hydrophone array if there was no 2D coordinate for more than 400 s. Following the approach of Brown et al. (2009), there were two ways the script assumed another visit to the hydrophone array. First, if there was a 2D coordinate outside of the hydrophone array and the fish subsequently was detected inside the hydrophone array, the script assumed another hydrophone array visit. Second, if there was no 2D coordinate for more than 400 s, and a 2D coordinate inside the hydrophone array subsequently occurred, the script assumed another visit to the hydrophone array.

Buffer analysis was applied to individual tracks using GIS-software (ArcGIS 9.2, ESRI, Redlands, USA) to estimate the area (m²) covered (i.e. explored) by individual fish (Cote et al. 2010) inside the hydrophone array. The buffer width was 0.5 m. The covered area included any given area only once. This means that a fish moving repeatedly over the same area on many occasions would have the same estimated covered area as a fish that visited the same area only once. Thus, covered area may not always vary with the travelled distance. The area covered is considered an index of exploratory tendency (Cote et al. 2010). Finally, the tortuosity of individual tracks was calculated using the mean fractal dimension (Nams 2006).

Similar to past studies (Buchanan et al. 2009), the positional analysis was restricted to smolts that entered the hydrophone array. This procedure allowed initial post-release handling mortality to be controlled for before the fish entered the hydrophone array (Buchanan et al. 2009).

The Wolf trap was situated 90 m downstream of the hydrophone array. Recaptured tagged smolts passed the water withdrawal zone successfully (Fig. 1). Using the recapture data from the trap, tracked smolts were divided into passing and non-passing smolts. Non-passing smolts having their last 2D coordinate inside the water withdrawal zone (Fig. 1) were assumed to have entered the fish farm through the debris racks.

Smolts visiting the hydrophone array only once were considered non-milling, while smolts visiting the hydrophone array more than once were considered milling. Comparisons of non-milling and milling smolts were confined to fish recaptured in the Wolf trap (i.e. passing smolts). This approach ensured that no fish included in the analyses had been preyed upon by piscivorous fishes.

2.5 Environmental factors

Daily amounts of river discharge diverted to the fish farm and passing over the weir crest were monitored following Svendsen et al. (2010). River temperature was measured hourly to nearest 0.01 °C using temperature loggers (TidbiT, Onset Computer, Bourne, USA).

2.6 Statistical analysis

Fisher's exact test was applied to compare proportions of the tracked smolts that entered the water withdrawal zone. Differences between non-milling and milling smolts were analysed using the Mann-Whitney U test. The same test was used to compare passing and non-passing smolts. Least square linear regression was used to examine the relationships between the number of visits to the hydrophone array and the covered area (m²). Multiple binary logistic regressions (likelihood ratio) with stepwise backward elimination (removal criteria: $\alpha > 0.1$) were employed for the probability of passage (i.e. recapture) as the dependent variable and the behavioural measurements as independent variables. Tests were carried out using SPSS 15.0 (SPSS Inc., San Rafael, CA, USA). Results were considered significant if $\alpha < 0.05$. All values are reported as means \pm s.e.m. unless noted otherwise.

3 Results

During the study period, the percentage of the total river discharge allocated to the fish farm was 20.7 \pm 6.7% (mean \pm SD). The entire volume of river discharge that passed the water withdrawal zone (Fig. 1) drained through the trap at all times.

A total of 61 tagged Atlantic salmon smolts (total length: 19.1 \pm 1.1 cm; body mass: 53.1 \pm 9.9 g) was tracked by the hydrophone array. Data from the Wolf trap revealed 41 recaptured smolts. The remaining 20 tracked smolts were not recaptured. No tagged smolts passed the hydrophone array without being tracked.

The passing (i.e. recaptured) smolts were divided into non-milling smolts (27 fish; 65.9%) and milling smolts (14 fish; 34.1%). Non-milling smolts performed only one visit to the hydrophone array (Fig. 2a), whereas milling smolts visited the hydrophone array repeatedly (Fig. 2b). On average, milling smolts performed 9.7 \pm 2.3 visits to the hydrophone array. Compared to the non-milling smolts, a larger proportion of the milling smolts entered the water withdrawal zone (Fisher's exact test; $p < 0.0001$) (Table 1). Moreover, milling smolts covered a larger area, spent longer time inside the hydrophone

Table 1. Data describing non-milling and milling Atlantic salmon (*S. salar*) smolts tracked near a water withdrawal zone in a lowland river. All variables, except body length, differed significantly between the two groups of smolts (all $p < 0.003$). Both non-milling and milling smolts were recaptured in the Wolf trap (see Fig. 1).

	Non-milling smolts	Milling smolts
Sample size (<i>n</i>)	27	14
Proportion entering water withdrawal zone (%)	3.7	64.3
Area covered (m ²)	42.7 \pm 1.0	168.7 \pm 33.6
Time (min)	2.7 \pm 0.4	112.2 \pm 30.6
Distance (m)	42.3 \pm 1.1	353.8 \pm 78.2
Travel speed (m s ⁻¹)	0.48 \pm 0.05	0.22 \pm 0.05
Tortuosity	1.03 \pm 0.01	1.30 \pm 0.04
Body length (cm)	19.0 \pm 0.2	19.3 \pm 0.3

array, migrated further, and travelled slower with increased tortuosity compared to the non-milling smolts (Mann-Whitney Tests; all $p < 0.003$) (Table 1). There was no body size difference between milling and non-milling smolts (Mann-Whitney Test; $p > 0.52$) (Table 1).

Using all the 41 recaptured fish, non-milling and milling smolts were combined to test for a relationship between the number of visits and the area (m²) covered by individual smolts. This analysis showed that the number of visits to the hydrophone array correlated positively with the covered area (linear regression; $r^2 = 0.90$; $n = 41$; $p < 0.0001$) (Fig. 3).

The relationship between number of visits and covered area was described using the equation $Y = a + bX$. In the equation, Y is the area (m²) covered by individual smolts, X is the number of visits to the hydrophone array by individual smolts, while a is 30.1 (\pm 5.4) and b is 13.9 (\pm 0.8). The equation is relevant for 1–29 visits to the hydrophone array (Fig. 3). Data showed that for each additional visit to the hydrophone array, individual smolts explored another 13.9 m².

The non-passing (i.e. not recaptured) smolts (20 individuals) were divided into tracks that ended inside the water withdrawal zone (20%; 4 individuals) (Fig. 2c) and tracks that ended elsewhere (80%; 16 individuals) (Fig. 2d). Smolt tracks that finished in the water withdrawal zone ended abruptly (Fig. 2c). It seemed reasonable to assume that these smolts entered the fish farm through the debris racks. There were few 2D coordinates from these smolts, and they were excluded from further behavioural analysis. Analysis of the remaining (80%) non-passing smolts and the passing smolts indicated substantial behavioural differences (Table 2). Compared to the passing smolts, the proportion of the non-passing smolts that entered the water withdrawal zone was significantly higher (Fisher's exact test; $p < 0.001$) (Table 2). Moreover, the covered area, the time spent inside the hydrophone array, the migrated distance, the number of visits to the hydrophone array, the travel speed and tortuosity all differed between the passing and non-passing smolts (Mann-Whitney U test; all $p < 0.001$) (Table 2). The body length of the passing and non-passing smolts did not differ (Mann-Whitney Test; $p > 0.81$) (Table 2).

Combining passing and non-passing smolts, the logistic regression indicated that time spent in the hydrophone array strongly influenced the probability of passage ($n = 57$; $p < 0.001$) (Fig. 4). The relationship between time spent in the

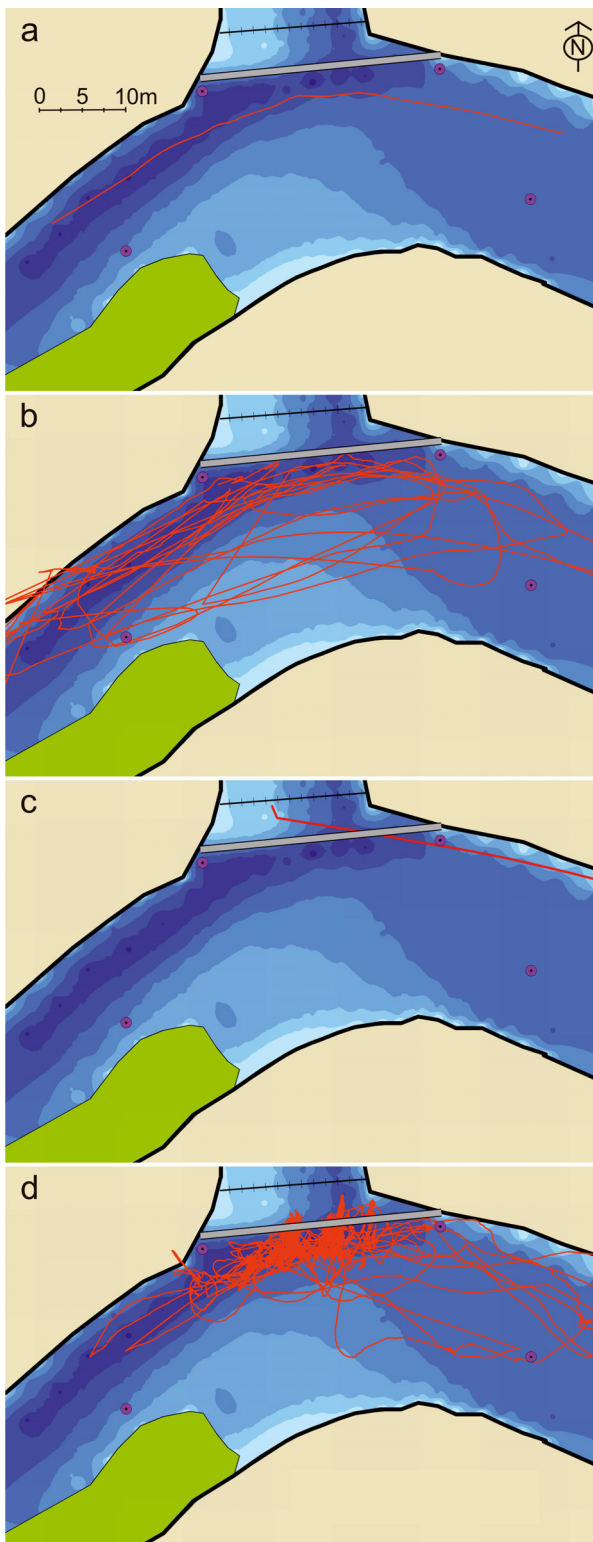


Fig. 2. Migratory routes of Atlantic salmon smolts approaching a water withdrawal zone in a lowland river (red lines). (a) A recaptured smolt having one visit to the hydrophone array (i.e. non-milling smolt). (b) A recaptured smolt having multiple visits to the hydrophone array (i.e. milling smolt). (c) A not recaptured smolt with a track that ended in the water withdrawal zone. (d) A not recaptured smolt that did not end in the water withdrawal zone. See Figure 1 for details.

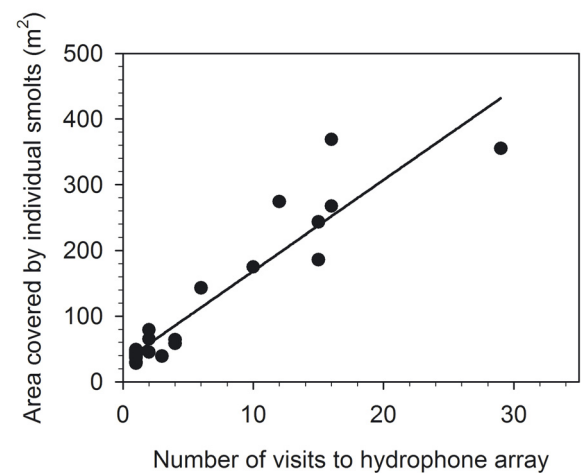


Fig. 3. Linear relationship between the number of visits to a hydrophone array performed by individual smolts and the covered area (m^2) ($n = 41$ smolts).

Table 2. Data describing passing and non-passing Atlantic salmon (*S. salar*) smolts tracked near a water withdrawal zone in a lowland river. Passing smolts migrated past the water withdrawal zone and were recaptured (see Fig. 1). All variables, except body length, differed significantly between the two groups of smolts (all $p < 0.001$).

	Passing smolt	Non-passing smolt
Sample size (n)	41	16
Proportion entering water withdrawal zone (%)	24.4	81.3
Area covered (m^2)	82.6 ± 13.9	388.6 ± 62.4
Time (min)	37.4 ± 12.4	2473.0 ± 714.8
Distance (m)	141.0 ± 33.3	2774.6 ± 722.7
Number of visits to hydrophone array	3.8 ± 1.0	73.0 ± 18.3
Travel speed (m s^{-1})	0.39 ± 0.04	0.11 ± 0.04
Tortuosity	1.11 ± 0.03	1.54 ± 0.06
Body length (cm)	19.1 ± 0.2	19.2 ± 0.3

hydrophone array by individual fish (t , hours) and the probability of passage (P) was described using the logistic equation $P = \frac{e^{a+bt}}{1 + e^{a+bt}}$. The equation ($a = 2.50(\pm 0.56)$ and $b = -0.36(\pm 0.15)$) indicated that the probability of passage correlated negatively with the time spent inside the hydrophone array (Fig. 4). For example, an increase in time from 1 h to 10 h decreased the probability of passage from 90% to 25%. The time at which 50% of the smolts passed was 6.9 h (Fig. 4). The model correctly assigned 93% of data. The range of time that the smolts were spending in the hydrophone array was 0.01–146.2 h.

4 Discussion

This study is among the first to quantify the behaviour of downstream migrating smolts using high resolution telemetry (Ehrenberg and Steig 2003; Goodwin et al. 2006; Nestler et al. 2008), particularly in shallow rivers. The results showed that

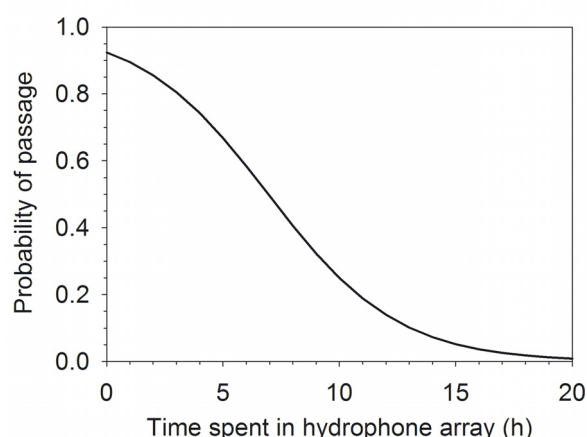


Fig. 4. Logistic relationship between time spent inside a hydrophone array and the probability of passage of a water withdrawal zone in a lowland river ($n = 57$ smolts). See Figure 1 for details.

Atlantic salmon smolts performing milling behaviours covered a larger area (m^2) (Fig. 3), and in turn experienced an increased probability of entering the water withdrawal zone, considered an adverse habitat (Table 1). Several behavioural traits differed between the non-passing smolts and the passing smolts (Table 2). In particular, time spent near the water withdrawal zone correlated negatively with the probability of passage (Fig. 4).

A number of studies have reported Pacific salmon smolts performing milling behaviours in anthropogenically altered channels (Venditti et al. 2000; Plumb et al. 2006; Nestler et al. 2008). The present study showed that milling behaviours also occur in Atlantic salmon smolts (Fig. 2b). Several behavioural variables differed between the milling and non-milling smolts (Table 1). In contrast, the body sizes of the two groups of smolts were similar (Table 1). The range of body sizes was, however, limited (17–22 cm) in the present investigation. Further studies testing relationships between body size and milling behaviour are required before any firm conclusions can be drawn.

Few studies have examined the consequences of milling behaviours. In the present study, the milling smolts differed considerably from the non-milling smolts (Table 1). The number of visits to the hydrophone array correlated positively with the covered area (Fig. 3). For each visit to the hydrophone array, individual smolts explored another 14 m^2 . This explorative behaviour increased the probability of exposure to the water withdrawal zone (Table 1). Although milling behaviours may enable fish to locate migration routes (Brown et al. 2009), milling behaviours may also have a number of negative consequences. First, milling behaviours may increase the probability of entering adverse habitats as demonstrated by the present study. The water withdrawal zone constituted the area where river water drained into the fish farm (Fig. 1). Smolts entering the water withdrawal zone and subsequently the fish farm are subjected to severe mortality because of the high density of adult rainbow trout in the ponds (Svendsen et al. 2010). Thus, the water withdrawal zone is considered an adverse

habitat (Svendsen et al. 2010). Second, milling behaviours are coupled with increased risk of predation by wild piscivores (McCormick et al. 1998; Venditti et al. 2000; Plumb et al. 2006). In the present study, the milling smolts covered a larger area, travelled longer, and spent longer time inside the hydrophone array (Table 1). Because of positive relationships between fish movement and predation risk (Martel and Dill 1995; Aarestrup et al. 2005), the milling smolts probably faced an increased risk of predation. Finally, milling behaviours are associated with additional energetic costs (Nestler et al. 2008).

A number of factors may influence the probability of passing a water withdrawal zone. A recent study developed a model to predict the probability of passage past the water withdrawal zone in the Konge River (Svendsen et al. 2010). The probability of passage was modelled as a function of the percentage of river discharge allocated to the fish farm. Increased allocation to the fish farm decreased the probability of passage. For Atlantic salmon, the model predicted that if the percentage of river discharge allocated to the fish farm increased from 38 to 68%, the probability of passage decreased from 64 to 36%. In the present study, 21% of the river discharge was allocated to the fish farm through the water withdrawal zone. Recapture of tracked smolts showed that 67% of the fish (41 out of 61) passed the water withdrawal zone successfully. The observed probability of passage (67%) is within the range (63–87%) predicted by the model. While the model highlighted the importance of river discharge allocated to the fish farm (Svendsen et al. 2010), the study did not provide the behavioural underpinnings of successful and unsuccessful passage of the water withdrawal site. The present tracking study was initiated to get a better understanding of the behaviour of Atlantic salmon smolts approaching the water withdrawal zone. For example, to what extent do smolts enter the fish farm? Svendsen et al. (2010) discussed the possibility that a fraction of the non-passing smolts may discontinue migration instead of entering the fish farm. The present study indicated that some smolts entered the fish farm (Fig. 2c), however this mechanism only accounted for 20% of all the non-passing smolts (4 out of 20). The remaining 80% of the non-passing smolts (16 out of 20) did not enter the fish farm, but paused downstream migration and were observed inside the hydrophone array for an extended period of time (Fig. 2d; Table 2). Thus, although the probability of passage correlates negatively with the river discharge allocated to the fish farm (Svendsen et al. 2010), fish entering the fish farm is not the only reason why some fish failed to pass the water withdrawal zone. This shows that fish passage is impaired by water diversion and not the presence of the fish farm *per se* (as most non-passing fish did not enter it).

In the past, downstream migration of smolts was thought to be largely a passive displacement with water flow (e.g. Smith 1982). More recent studies have however, demonstrated smolts responding behaviourally to in-stream structures (Kemp and Williams 2008) and visual clues (Kemp and Williams 2009), avoiding rapidly accelerating currents (Haro et al. 1998; Enders et al. 2009) and overhead cover (Kemp et al. 2005), and preferring certain areas while migrating downstream (Davidsen et al. 2005; Svendsen et al. 2007). The present study corroborates the conclusion that smolt migration includes active components and depends on behavioural

decisions. First, smolts performed milling behaviours that included upstream swimming (Fig. 2b). As smolts continued to visit the hydrophone array, they expanded the covered area (Fig. 3), probably reflecting explorative behaviour. Second, there were significant behavioural differences between passing and non-passing smolts (Table 2). These findings highlight the active component in smolt migration and call for fish passage solutions that include behavioural considerations.

The exact fate of the non-passing smolts (Table 2) remains unknown. Smolts undergo a preparatory process involving several physiological and morphological changes directed towards optimising the performance in the marine environment (McCormick et al. 1998; Nielsen et al. 2001). The physiological changes correlate with migratory activity (Strand et al. 2011) and sea water tolerance (Nielsen et al. 2001). The non-passing smolts may have reverted to the parr condition (i.e. desmoltification) because they remained in the river (McCormick et al. 1998; Todd et al. 2011). Juvenile Atlantic salmon post-smolts that remain in freshwater and revert to the parr condition may return to the smolt condition in subsequent years (Shrimpton et al. 2000). It is possible that the non-passing smolts continued downstream migration in the following spring, however additional studies are required to test this hypothesis.

This study indicated migratory delays associated with the passage of the water withdrawal zone. Passage of the milling smolts was significantly delayed compared to the non-milling smolts (Table 1). The non-passing smolts appeared to discontinue downstream migration, perhaps until the following spring. Migratory delay may have detrimental effects for smolts. The most significant determinant of the passage probability was the time spent in the hydrophone array (Fig. 4). For example, smolts that delayed the passage of the water withdrawal zone from 1 h to 10 h simultaneously decreased the probability of passage from 90% to 25% (Fig. 4). In support of recent studies (Kemp and O'Hanley 2010; Petrosky and Schaller 2010), these findings call for management actions that minimise migratory delay in anthropogenically altered channels.

The present work did not relate smolt behaviour to any environmental or seasonal conditions because of three study constraints: (i) the environmental conditions varied little during the study period. For example, most fish were released when the percentage of the total river discharge allocated to the fish farm was $20 \pm 6.7\%$ (mean \pm SD). In no cases was more than 31% of the river discharge allocated to the fish farm; (ii) river discharge was only measured daily. This temporal resolution was considered insufficient to test relationships between river discharge and the behaviour of the fish; (iii) the study period was relatively short and did not include the early and late migrating smolts. Finally, it was beyond the scope of the present work to manipulate the conditions experimentally.

5 Conclusion

The goal of this study was to examine the behavioural underpinnings of passage of a water withdrawal zone in a shallow river. The results indicated a relationship between milling behaviours and the probability of exposure to an adverse habitat.

The more visits individual fish performed to the hydrophone array, the larger area they covered. In turn, the repeated visits translated into an increased probability of exposure to an adverse habitat. In addition, the results indicated significant behavioural differences between the passing and non-passing smolts in this shallow river. In particular, the results suggested that passage time past the water withdrawal zone was an important determinant of passage probability.

This study demonstrated that factors delaying smolt migration may be important determinants of the probability of passage. If approaching smolts are repelled by the water withdrawal zone, guided towards the weir, and attracted to passing over the weir crest, passage time may be minimal. Thus, it is possible that passage time can be reduced by management measures that induce these behaviours. Recent studies have demonstrated behavioural avoidance in smolts related to hydraulic conditions (Haro et al. 1998; Enders et al. 2009), in-stream structures (Kemp and Williams 2008), overhead cover and absence of visual clues (Kemp et al. 2005; Kemp and Williams 2009). Moreover, fish guidance may be accomplished using strobe lights (Johnson et al. 2005), bubble curtains and sounds (Welton et al. 2002; Sonny et al. 2006) and deep, mid-channel furrows (Svendsen et al. 2007). These findings indicate that smolts can be guided rapidly past the water withdrawal zone and over the weir crest to ensure passage.

The marine growth and survivorship of Atlantic salmon depend on complex relationships between ocean climate and epipelagic prey availability (Hvidsten et al. 2009; Todd et al. 2011). The marine survival is generally density-independent (Jonsson and Jonsson 2004), and the number of returning mature fish is usually proportional to the number of smolt emigrants (Crozier and Kennedy 1993; Jonsson et al. 1998). This means that a loss of fish at the smolt stage adversely affects adult recruitment (Johnsen et al. 2011). Conversely, it is possible that fast passage past adverse habitats during downstream migration may promote more adult fish returning to spawn.

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